Technical Report No. 34

FLORISTIC AND STRUCTURAL DEVELOPMENT OF NATIVE DRY FOREST STANDS AT MOKULEIA, N.W. OAHU

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U. S. International Biological Program

January 1974

PREFACE

The following investigation relates to a reanalysis--after twenty years--of a tropical lowland to submontane forest on the island of Oahu. The forest occurs in a summer-dry climate with a Mediterranean rainfall pattern. It thus can be considered a "tropical seasonal forest." This forest is unique insofar as it represents a relict vegetation with a dominance of native island tree species in a vegetation zone that is elsewhere completely converted to introduced vegetation. The results of this study are of particular interest to the ISLAND ECOSYSTEMS IRP since they are concerned with the stability-fragility question complex of island vegetation.

The report represents the major part of a Master of Science Thesis in Botanical Sciences carried out under the direction of D. Mueller-Dombois. The study was initiated under NSF Grant GB-4688. The major support came from the McIntire-Stennis fund for forestry research held by the Hawaii Agricultural Experiment Station of the University of Hawaii. The work was completed with funds from the ISLAND ECOSYSTEMS IRP, NSF Grant GB-23230.

ABSTRACT

Almost all species recorded 20 years ago from seven plots of native dry forest stands at Mokuleia are still found in their respective plots. Except in two plots, almost all the dominant native species are regenerating and maintaining themselves. The regeneration of native *Canthium odoratum* is curtailed by a moth (*Orneodes objurgatella* Walsingham) which infests and kills embryos of *Canthium*. Introduced *Schinus terebinthifolius* trees have invaded the plot and have also suppressed the native *Canthium* trees. The seedling establishment of native *Erythrina sandwicensis* was handicapped by the invasion of an introduced grass *Melinis minutiflora* which covers the ground densely. Other new introduced species invaded almost all plots, whereas new native species invaded only plots located in or near the Mokuleia Forest Reserve, the main sources of native species in this area. If undisturbed by animals or fire, native forests can maintain themselves. However, shade-tolerant introduced species seem to remain as minor component in these native forests. Among the native species, *Sapindus oahuensis* is able to invade the introduced *Leucaena leucocephala* stands, where *Sapindus* can become the dominant tree cover. To reclaim the dry lowland areas with native forest trees, *Sapindus* seems to be one of the species of promise.

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INTRODUCTION

The present study is a re-analysis of Hatheway's sample plots in the dry forest stands at Mokuleia (Hatheway 1952). It is carried out 20 years after the first analysis was made. The reconnaissance and the analysis of these sample plots were started in the summer 1970 and the analysis of all the plots was completed in the spring 1971. The objective of this study was to find if floristic and structural changes of vegetation had occurred during this period, especially in relation to the status of the present native and introduced Hawaiian plant species.

In this study, introduced species are defined as species that are known to have been brought to these islands by man and native species as species that arrived in these islands without the aid of man. The native forest is defined as the plant cover composed of trees taller than 4 m, with interlocking crowns, and with more than 50% of the total basal area contributed by native tree species. The dry forest as defined by Hatheway and used in this paper essentially belongs to the xero-tropical zones and to the lower portion (Guava zone) of the pluvio-tropical zones of Egler (1939). Instead of the 125 cm (50 inches) isohyet used by Egler in differentiating between the vegetation of xero-tropical (dry forest) and pluvio-tropical (rain forest), Hatheway used the physiognomy of the ground layer, which can be easily identified in the field. The dry forest was defined as having bare ground and the rain forest as having a dense undergrowth covering the ground.

Literature review

The vegetation of Egler's (1939) xero-tropical zones and the lower portion of the pluvio-tropical zones of Oahu form the bulk of the vegetation in the lowlands and on the leeward side of this island. Due to the introduction of goats and cattle by Europeans since Captain Cook discovered the Hawaiian Islands in 1778, the native Hawaiian vegetation in these zones has been severely disturbed. By now, this native vegetation has been almost completely replaced by purposely or accidentally introduced plant species that spread out from gardens and cultivated areas. Only a few patches of native vegetation remain on some steep slopes or in other topographically protected lowland areas (Degener 1930, Egler 1939, 1942, Fosberg 1961). However, native vegetation is still prevalent in some coastline habitats (de Ausen 1966), in the montane rainforest on all mountainous islands (Fosberg 1961, Degener 1930, Krajina 1963), on new volcanic substrates on the island of Hawaii (Doty and Mueller-Dombois 1966), and in the subalpine and alpine regions on the two high elevation islands, Maui and Hawaii (Fosberg 1959, Mueller-Dombois 1967, Mueller-Dombois and Krajina 1968).

Degener (1930) and Carlquist (1965) believed that native species lacked the ability to compete with the introduced plant species. They suggested that the native Hawaiian flora will become extinct. However, Egler (1942, 1947) and Hatheway (1952) held that the introduced plant species do not necessarily replace the native species. They predicted that, in the absence of anthropic disturbance, most introduced species would be replaced again by native species which then would perpetuate themselves indefinitely.

Forests provide an important protective cover against accelerated soil erosion in the rugged Hawaiian Islands and forest cover has an important function in the island ecosystem as a whole. Forests of native Hawaiian plant species are of particular value in this regard, because: (1) Native forests provide habitats for other native biota. The evolution of the native Hawaiian fauna has been directly related to the evolution of the native Hawaiian flora (Carlquist 1965, 1970, Spieth 1966). Loss of the native forests results also in loss of the associated native biota. (2) The native Hawaiian fauna and flora are unique in the world. They have unique insular evolution characteristics (Zimmerman 1948, Carlquist 1965). Population sizes of many insular species are small, and size reductions of such populations may easily lead to extinction. (3) The native Hawaiian forests may hold values that are as yet uncovered by research. Only recently Acacia koa ("koa") has received greater attention because of the value of its wood for fine quality furniture. Moreover, other values may be discovered that are not yet known. For example, the bark of Ochrosia sandwicensis ("holei"), a rare native species, contains alkaloids that, from preliminary investigations, may have a high potential as anti-carcinogens (Jordan and Scheuer 1965, Scheuer personal communication). Extinction of native Hawaiian plant species, therefore, would be an irreplaceable loss in view of the many possible and unknown properties that they hide.

Better understanding of the development of the present native and introduced Hawaiian vegetation is, therefore, very important for intelligent management of this unique insular ecosystem. Hatheway's work (1952) was the first ecological study, based upon sample plots, carried out on this island. Other studies were mainly based on general observations which were hard to duplicate. Hatheway's work was carried out in the native dry forest stands at Mokuleia and was mainly based on data collected from seven sample plots. This study provided a good opportunity to derive new information on the development of native dry forests. Re-analyzing Hatheway's plots and comparing the new results with his was thought to be useful before carrying out more intensive studies in this area.

Hatheway's analysis

To study the floristic composition of the native dry forest at Mokuleia, Hatheway selected seven stands with native trees. In each of these stands he established a sample plot. In each plot he counted the number of individuals of each woody plant species, native and introduced, that were larger than 2.5 cm in diameter. He recorded these in diameter classes. From these records he calculated the basal area of each species. In this way, he showed some quantitative relationships between the introduced and native Hawaiian species.

Based mainly on the floristic composition, leaf-fall pattern, and structure of forest stands in this area, Hatheway recognized two types of vegetation cover. He named these evergreen seasonal and semi-deciduous seasonal forests. In his study, plot 7 was classified as representing the evergreen forest type and plots 4, 5, and 6 as representing the semi-deciduous forest type. To verify Egler's view (1942) that native species may be able to invade and replace stands composed of introduced plant species, he established plots 1, 2, and 3 as examples of seral stands that contained some immature native trees. The structures of these forests and seral stands are summarized in Table 1.

Based on the results of his analysis in each plot and the information derived from his general observation in the Mokuleia area, Hatheway concluded that the two native forest types he had recognized and described would replace the introduced forest or scrub vegetation that covered most of the lowland areas of Oahu. Once these native forests became established, he believed that they would perpetuate themselves indefinitely in the absence of disturbance.

GENERAL DESCRIPTION OF STUDY AREA

Geography

Oahu is one of the islands in the Hawaiian Archipelago. It has two mountain ranges that are more or less parallel to each other in the SE-NW direction. The Koolau Range, 55 km long and 16 km wide, forms the eastern part of the island and the Waianae Range, 32 km long and 13 km wide forms the western part. Mt. Kaala, 1028 m, is the highest peak of the Waianae Range and is also the highest point on this island (Stearns 1966).

TABLE 1. -- Hatheway's plot analyses. Summary of the forest and seral stand structures of the seven plots.

Vegetation type	Evergreen forest	Semi-deciduous forest			Seral stand		
Plot no.	7	6	5	4	3	2	1
Dominant species	Diospyros Metrosideros Canthium	Diospyros Canthium	Sapindus	Sapindus	Erythrina*	Canthium	Sapindus Leucaena*
Forest canopy	closed	open	open	closed	closed**	open	closed**
Height of forest canopy	10.5 m	10 m	10-14 m	13 m	----	----	4-5 m
Undergrowth	sparse ferns and sedges	Lantana	sparse herbs	sparse herbs	Rhynche-lytrum	Rhynche-lytrum + Lantana	----

* Summer-deciduous species
** Open during the summer or dry season

Mokuleia, as defined by Hatheway and used in this paper, is the north-facing slope of the north-west end of the Waianae Range. The area extends from the main crest to the ocean and from the East Makaleha Valley to Kealia (Fig. 1).

Geology

The parent material of the substrate in this area is composed of three basaltic lava flows that originated from eruptions in the Tertiary period. The upper portion of the first and the second series of lava flow consists primarily of thin-bedded pahoehoe. But more a'a is associated with the second series. The third and youngest lavas are mostly massive a'a andesite flows (Stearns and Vaksik 1935, Stearns 1966, MacDonald 1940). From the distribution map of these three series of lava flows (ibid.) and the map of the plot locations given by Hatheway, two of the seven plots of Hatheway, numbers 2 and 3, were located on the last type of flow whereas all the other plots are on the first two types.

Topography

The north facing slope of the Mokuleia area is cut by many ephemeral streams that run northward from the main crest of the Waianae Range forming steep gulches and narrow ridges that are more or less parallel to each other.

Soil substrate

In spite of the differences in types of parent material in this area, Hatheway described only one type of substrate whereas Cline (1955) recognized two main types. The Humic Ferruginous Latosol (and its eroded remnant) of Cline, which was probably recognized by Hatheway as immature stages of the Humic Latosol, covers only a small portion of this area. The larger portion is covered by Lithosol, which is rockland or rough, broken land without or with only a thin layer of soil. Hatheway's plots 2 and 3 are located on the Humic Ferruginous

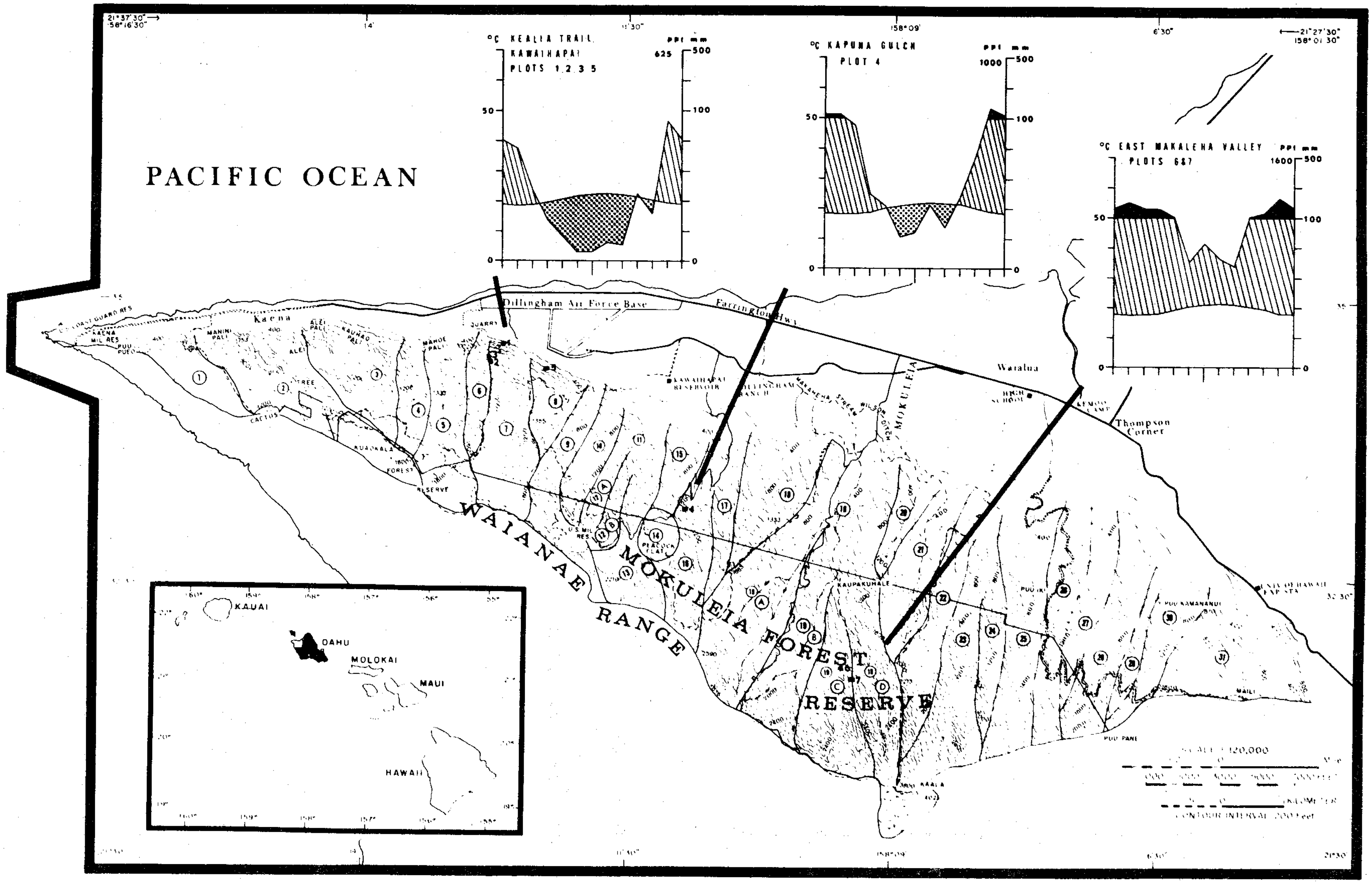


Fig. 1. Topographical map of Mokuleia with plot locations and climate diagrams. Square dots (■) with numbers indicate the location of plots. Numbers within circles indicate gulches. The study area extends from the main crest of the Waianae Range to the ocean and from Makaleha Valley (19), East Branch (D), to Kealia between gulch 6 and 7.

Latosol. The rest of the plots are located on the Lithosol type. Of these, plots 1 and 5 are located on big rubble-rocks (colluvial material) on steeply sloping talus. Plot 4 is isolated on rockland that has a thin layer of soil. Plots 6 and 7 are located on rough broken land with a deeper soil and higher humus content.

Vegetation

The slopes around the top of Mt. Kaala, where much wetter conditions prevail, are covered by a sub-montane rain forest characterized by the dominant *Metrosideros collina* subsp. *polymorpha*. This area forms the major and upper part of the Mokuleia Forest Reserve. There is a flat lowland zone along the coast which is mostly used as sugarcane plantation. Here the soil is deep with hardly any rock outcrops. The dry forest with Hatheway's plots is found between these two zones. This in-between area is not uniformly covered by forest. It includes the lower portion of the Mokuleia Forest Reserve (below 700 m elevation) and the ranch areas (Kaala and Mokuleia Ranches) which are covered by grass, scrub, and forest in irregular patterns. Plots 6 and 7 are located in the forest reserve whereas the other plots are in the forested ranch terrain. Except for certain less accessible slopes or slopes in the forest reserve where native Hawaiian plant species (e.g. *Diospyros sandwicensis* and *Sapindus oahuensis*) are found, the species in the scrub and forest stands are mostly introduced. The more important introduced trees are: *Leucaena leucocephala*, *Eugenia cumini*, *Psidium guajava*, *Psidium cattleianum* and *Schinus terebinthifolius*. In addition, forest trees have been planted in some areas. These include *Grevillea robusta*, *Araucaria excelsa*, *Eucalyptus* spp., etc. The bottoms of the gulches are occupied mainly by *Aleurites moluccana*, which can be easily recognized by its light green canopy.

History

The documents on the Mokuleia Forest Reserve (Forestry Division, 1918-cont.)

revealed that the Mokuleia area has long been used for cattle grazing by a number of ranches. Although the upper portion of this area has been set aside as the Mokuleia Forest Reserve and as such has been separated from the remaining ranch areas by a fence since 1918, cattle still roamed this forest reserve until 1922. During the second World War, when these ranches were less well controlled, cattle once again strayed in this forest reserve. It was only in 1947 that all wild cattle were killed or brought back into the fenced ranch area. Since this time, only goats and pigs (although probably not many) still remain in this forest reserve.

Hatheway's plots were established in 1950/1951. His plots 6 and 7 are located in the forest reserve. Therefore these two plots have been free from cattle since they were established. In contrast, his plots 1, 2, 3, 4, and 5 are located in the ranch areas outside the reserve and are still in the reach of stray cattle.

Climate

The study area has a warm tropical climate, with mean January and July temperatures at Kawaihapai (6 m alt.) 22°C and 25°C respectively (U. S. Weather Bureau 1953). The wet or rainy season extends from November to April. During this time the east-northeasterly tradewinds slacken and the southerly Kona (leeward) storms become prevalent. The dry season generally starts in May and ends in October. The elevation of the area, in general, is too low to intercept much water vapor from the tradewinds that are prevalent during this period (Price 1966, Blumenstock and Price 1967, Carlquist 1970). However, there is a significant increase on the amount of rainfall with increasing elevation. At the top of Mt. Kaala for example, the annual rainfall is about 2,500 mm. At lower elevations a few kilometers away, for example at Kawaihapai, the annual rainfall is only 750 mm (U. S. Weather Bureau 1953). Using Walter's method (Doty and Mueller-Dombois 1966), climate differences between Hatheway's plots are shown by three climate diagrams found in Fig. 1. The rainfall data were obtained through extrapolation from rainfall maps of Taliaferro (1959). The monthly temperature records at different altitudes were extrapolated from the records of Waialua Weather Station (10 m alt.) (U. S. Weather Bureau 1953). The adiabatic lapse rate used here was 0.8°C per 100 m increase in altitude (Kartawinata 1971).

METHODS

Field procedure

The results of the present analysis and their validity for comparison with Hatheway's depended very much upon the accuracy of relocating Hatheway's plots. The approach adopted for this purpose used a combination of information, such as, the locations as indicated on Hatheway's map diagram, described coordinates, altitudes, and floristic composition of each plot, and the photos and topographical map as given by Hatheway. In addition, the 1964 USGS topographical map and the 1950, 1969, and 1971 aerial photographs were also used. These plot locations are shown in Fig. 1.

Steep, rugged terrain made walking in the area difficult. An efficient sampling method, therefore, would require the least amount of walking. A comparison between a number of widely used sampling methods for measuring density and basal area by Lindsey (1958) showed circular plots (400 m^2 in size) outlined with a rangefinder to be one of the most efficient sampling units. With a modification of the size of the circle, made necessary because of the different sizes of Hatheway's plots and required by the terrain, this method proved best for this study. The absence of dense undergrowth in these forests made the use of a rangefinder possible. Table 2 shows the sizes and elevations of the present plots as compared with Hatheway's.

Data analysis

Changes of forest structure were studied by checking in the field the forest structure described by Hatheway and also by comparing the air-photos taken in 1950 (the time of Hatheway's study) with the ones taken in 1969 and 1971.

The present analysis includes counting and measuring for size all individuals of woody plants found in each plot, even the ones smaller than 2.5 cm in diameter. This is an expansion over the analysis of Hatheway who recorded only from this size limit and upwards. Records of seedlings and small saplings are very important in understanding the maintenance trends of species. Individuals of each species were grouped into size classes. For practical purposes, plants below 2 m tall were recorded in height classes, plants above 2 m in diameter classes. The ranges of height and diameter classes are listed in Table 3.

The density and basal area values of each species were calculated in the same way as Hatheway. Hatheway used 2.5 cm (1.0 inch) diameter as the lower limit for calculation. In the present study, this lower limit is more or less the mid-point of diameter class 1 (plants below 3.8 cm or 1.5 inches diameter) in plots 1, 3, and 5 and the mid-point of diameter class 2 (plants between 1.3 - 3.8 cm or 0.5 - 1.5 inches diameter) in plots 2, 4, 6, and 7. For comparison, the computation of density and basal area of the new data was also made from 2.5 cm on upwards. Half of the number of trees in diameter class 1 (plots 1, 3, and 5) or in diameter class 2 (plots 2, 4, 6, and 7), in addition to all trees above each of these diameter classes were used in the present computation. The comparison between the 1950 and 1970 density and basal area values may shed some information on the maintenance trends of the species in these plots.

TABLE 2. -- Sizes* and elevations of plots as used by Hatheway (1950) and the present study (1970).

Plot no.	Location	Size (m^2) 1950	Size (m^2) 1970	Elevation (m) 1950	Elevation (m) 1970
1.	Kealia Trail	30	100	78	84
2.	Kealia Trail	1000	50(8)**	306	300-323
3.	Kealia Trail	200	400	279	282
4.	Kapuna Gulch	400	600	354	354
5.	Kawaihapai	1000	400(3)**	90	96-126
6.	Makaleha Valley	400	300(2)**	384	405
7.	Makaleha Valley	1000	200(5)**	546	510-546

* Hatheway did not indicate that he applied a slope correction factorto his plot size, the normal procedure used in forestry. However, the distribution of trees that Hatheway most likely recorded suggests that he may have used this correction factor. The 1970 plot sizes listed here incorporate slope corrections.

** A figure in parentheses refers to number of sub-plots.

TABLE 3. -- The ranges of height and diameter classes.

Size class	Range (cm) as used in Plot 1, 3, 5	Range (cm) as used in Plot 2, 4, 6, 7
	HEIGHT CLASSES (plants below 2 m tall)	
1	below 10	below 10
2	10 - 30	10 - 25
3	30 - 100	25 - 50
4	100 - 200	50 - 100
5	-------------	100 - 150
6	-------------	150 - 200
	DIAMETER CLASSES (plants above 2 m tall)	
1	below 3.8	below 1.3
2	3.8 - 6.3	1.3 - 3.8
3	6.3 - 8.8	3.8 - 6.3
4	8.8 - 11.3	6.3 - 8.8
5	11.3 - 17.5	8.8 - 11.3
6	17.5 - 22.5	11.3 - 13.8
7	22.5 - 27.5	13.8 - 16.3
8	27.5 - 32.5	16.3 - 18.8
9	32.5 - 37.5	18.8 - 21.3
10	37.5 - 42.5	21.3 - 23.8
11	42.5 - 47.5	23.8 - 26.3
12	47.5 - 52.5	26.3 - 28.8
13	52.5 - 57.5	28.8 - 31.3
14	57.5 - 62.5	31.3 - 33.8
15	62.5 - 67.5	33.8 - 36.3
etc.	etc.	etc.

A stable forest is one in which the dominant tree species perpetuate themselves. A self-perpetuating species is one that has individuals distributed in all life stages, from seedlings to mature trees (Bray 1956). Their population structure characteristically shows an inverse J-shaped distribution (Hough 1936, Meyer 1952, Leak 1965, Hett and Loucks 1971) in which the number of individuals within a given size class (frequency) declines curvilinearly with increase in size class. The logarithm of the number of individuals (log. frequency) characteristically declines linearly with increase in size class (Daubenmire 1968).

In the present study, log. frequencies were plotted against size class, in both height and diameter, for both the 1970 data and Hatheway's 1950 data. For convenience in comparing the class frequencies, which had varying class intervals, the largest class size was taken as a standard. The frequencies in each smaller class were then adjusted to represent the number of individuals that would be found if the class size was the same as the standard (standardized class). The adjustment factor in each case is simply the standard class size divided by the width of the particular class. The largest size classes are 100 cm (for plots 1, 3, and 5) and 50 cm (for plots 2, 4, 6, and 7) intervals for height classes and 5 cm (for plots 1, 3, and 5) and 2.5 cm (for plots 2, 4, 6, and 7) intervals for diameter classes. Because of this adjustment, the vertical axis does not refer directly to the actual number of individuals per 100 m^2, except for the larger size classes. The graphs slightly exaggerate the decline of log. frequencies of individuals with increasing size class because class number has been plotted linearly on the horizontal axis, although the first few classes are smaller than the rest. This scale of classes is, however, close to a linear scale of increasing plant age.

A self-perpetuating species is here defined as one showing decrease in log. frequency with increase in size class for both height and diameter or one showing a similar trend of log. frequency distribution in both the 1950 and 1970 diameter class. A decrease in log. frequency of height classes indicates that a species is regenerating. A decrease in log. frequency of diameter classes means that the species is maintaining itself. A declining species often shows an increase in the log. frequency with increase in the lower size classes.

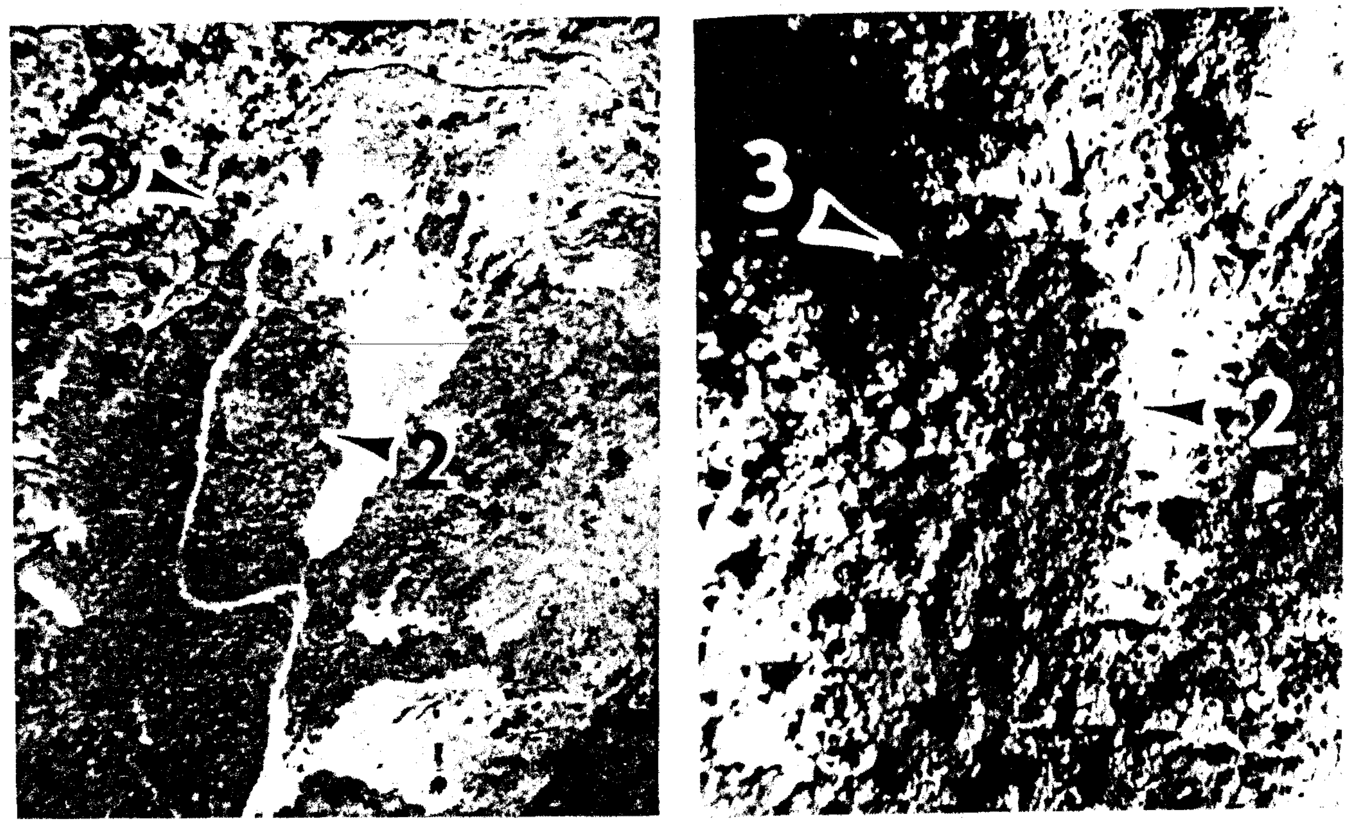
RESULTS AND DISCUSSION

Structural changes

The comparison of the 1950 air-photos with those of 1969 and 1971 shows, in general, an increase of vegetation cover in each of Hatheway's plots during the last 19 - 20 years. This change is very significant in the seral Canthium stand (plot 2, Fig. 2). Here, the scattered dots of Canthium odoratum on the grass-scrub matrix have changed into a closed woody plant cover. Due to this change, the Kealia Trail, which is clearly shown on the 1950 air-photo and is still in use or at least can still be recognized in the field as the former trail, cannot be seen on the 1969 air-photo. To a lesser degree, this increase of plant cover is also true with the other seral stands (plot 1 and probably also plot 3) and the semi-deciduous seasonal forest stands (plots 5 and 6). Although an increase of plant cover is also observed in the surroundings of plots 4 and 7, the semi-deciduous forest stand in plot 4 and the evergreen forest stand in plot 7 are probably not much changed. Furthermore, comparison of the forest structure and physiognomy of these plots as described by Hatheway and as observed in the field during this study support the results of the air-photos study. Starting with the semi-deciduous forest plots, the following are some changes of forest structure that were observed in the field.

Semi-deciduous forest stand dominated by native Diospyros and Canthium, plot 6.

In this plot and its vicinity, the formerly common Lantana camara has now



1950 1969

Fig. 2 -- Comparison between the 1950 and 1969 air-photo of plot 2. The increase of vegetation cover made the Kealia Trail, which is clearly shown in the 1950 photograph, unrecognizable in the 1969 photograph.

become scarce. Two of the lantanas found in the present analysis are extraordinarily large and tall. They grew like lianas with most of their dying branches suspended in the canopy of Diospyros sandwicensis, 3 - 5 m above the ground. The diameter of their stems were about 2.5 cm. It is possible that these plants were actually the remnants of the old Lantana population described by Hatheway. As Lantana is generally associated with open places, this fact supports the 1950 and 1971 air-photo comparison that the canopy of this forest stand was actually more open twenty years ago than it is now. The former open forest canopy described by Hatheway has now become a closed canopy, although Reynoldsia sandwicensis, which contributes a small portion of the canopy, sheds its leaves completely during the summer.

Semi-deciduous forest stand dominated by native Sapindus, plot 5.

A similar development of forest canopy, as in plot 6, was observed in this plot. The open forest canopy, an almost park-like appearance as described by Hatheway, is now essentially a closed forest canopy. However, Sapindus oahuensis, the major component of this stand, drops a greater part of its foliage during the summer-dry season together with the deciduous Reynoldsia sandwicensis, which is a less abundant species in this plot. The floristic composition of the ground cover is still similar to that described by Hatheway, except for the new record of a geophyte, Mirabilis jalapa. This species, an introduced ornamental plant, forms almost a closed ground cover during the wet season but its shoots disappear temporarily during the summer-dry season. One part of the plot showed an opening most likely caused by a fallen large Reynoldsia tree. This opening has now been filled with introduced species such as, Leucaena leucocephala, Lantana camara, Carica papaya, and the vine Ipomoea alba.

Seral *Erythrina* stand, plot 3.

The *Erythrina* stand in this plot occupied about 500 m^2 of the slope near the summit of the Kealia cliffs. Its single layer canopy was 5 - 7 m high. The ground cover which formerly was dominated by the grass *Rhynchelytrum repens*, is now almost completely replaced by *Melinis minutiflora*, a grass introduced to the island in 1913 (Whitney, et al. 1939). *Melinis* covered more than 75% of the ground. Tree seedlings were excluded from these thick and tall (about 1 m high) patches of *Melinis*. Tree seedlings were only found between patches and on bare ground under tall *Canthium odoratum* and dense *Erythrina sandwicensis*. These tree seedlings included *Erythrina sandwicensis*, *Eugenia cumini*, *Schinus terebinthifolius*, and *Leucaena leucocephala*. The tree seedlings were observed during the summer when the tree canopy was almost completely open. In the spring when little light was able to penetrate the then closed canopy, the greater portion of the *Melinis* cover died and seedlings of *Erythrina* were growing in these patches of dead *Melinis* (Fig. 3). But when *Melinis* had almost completely re-covered the ground by the middle of the following summer, none of these *Erythrina* seedlings were found. This observation supports the view expressed by Kartawinata (1971) that *Melinis minutiflora* is able to invade open plant communities and when established prevents other plants or seedlings from growing underneath it. As will be shown later, this is probably the main reason why only a few *Erythrina* seedlings and saplings (below 2 m) are now present in this stand.

Seral *Canthium*-*Leucaena* stand, plot 2.

Hatheway's prediction that the grass-scrub vegetation in plot 2 will be replaced by a forest composed of several species has started to come true within the twenty year period. There is very little *Rhynchelytrum repens* and *Lantana camara* now left in this forest stand. Patches of these two species left outside

Fig. 3 -- The ground cover of plot 3 in spring 1971. Seedling of Erythrina sandwicensis (with broad, ovate leaflets) sprouting in a patch of dead Melinis minutiflora. The grass at the lower left corner is part of the living Melinis.

the stand are now being invaded and covered by Melinis minutiflora. The photograph in Hatheway's paper and also the 1950 air-photo (Fig. 2) show that Canthium odoratum occurred only as scattered individuals in the grass-scrub matrix. However, due mainly to the increasing numbers of Leucaena leucocephala individuals, the present woody plant stand is very dense. Its biomass is distributed more or less evenly from the ground surface to the top of the canopy, 4 - 5 m above the ground. It forms a thick and closed cover during the wet season but is rather open during the dry season when Leucaena has shed its leaves. In addition to the seedlings of woody plants, herbaceous and semi-woody plants occasionally found in this stand were the native Cocculus ferrandianus (a vine), Sida fallax, and the introduced Sida spinosa, Cassia leschenaultiana, Setaria geniculata, and Stachytarpheta jamaicensis. An exception was found underneath the closed canopy of mature Schinus terebinthifolius trees, where nothing was growing on the ground, not even Schinus seedlings. The ground was thickly covered (up to 20 cm depth) by the leaf litter of Schinus.

Seral Sapindus stand, plot 1.

Hatheway's prediction for plot 1 has also come true. Saplings of the native Sapindus oahuensis that had invaded the Leucaena leucocephala stand in this area, as observed by Hatheway, have now become mature trees and overtop the introduced Leucaena stand. The foliar biomass of Sapindus trees forms a closed canopy at about 12.5 m above the ground. The biggest Sapindus tree was 55 cm in diameter. The size of Leucaena had also increased. The biggest Leucaena tree was 10 cm in diameter and 10 m high. The smooth, even canopy of Leucaena trees is closed during the wet season and open during the dry season. However, the closed canopy of Sapindus seems to exclude Leucaena from growing underneath it. Although germinants of Leucaena are abundant under the Sapindus canopy, none of them become established mature individuals. As observed in plot 5, almost no Leucaena was found under the canopy of Sapindus, but a number of young Sapindus may be seen in the Leucaena stand outside the plot, even on a slightly different substrata. Fig. 4 shows Sapindus growing on different kinds of habitats.

Floristic changes

Tables 4 - 10 list woody plant species, their basal areas, and densities, as recorded by Hatheway and the present study, for plots 1 - 7. The basal area and density values were compared on the basis of Hatheway's plot sizes. From these tables, changes of floristic composition, basal area, and density over the period of twenty years can be seen and calculated readily.

Native species.

Most of the native species recorded by Hatheway are still found in the present plots. Among them are 17 of the 18 native species that were in plot 7 in 1950 (Table 4), nine of the 11 native species that were in plot 6 in 1950 (Table 5), both the two native species that were in plot 5 in 1950 (Table 6), six of the eight native species that were in plot 4 in 1950 (Table 7), both the two native species that were in plot 3 in 1950 (Table 8), two of the three native species that were in plot 2 in 1950 (Table 9), and one of the two native species that were in plot 1 in 1950 (Table 10). Dracaena aurea (plot 6, Table 5) and Charpentiera obovata (plot 4, Table 7) were not measurable for diameter because their stems and branches were broken off and did not reach the 2 m height limit. Some of their stems near the ground surface, however, were larger than 2.5 cm in diameter suggesting that they may have been part of the population recorded by Hatheway. In addition, some of the species missing in 1970, for example Xylosma hawaiiensis (plot 7, Table 4) and Erythrina sandwicensis (plot 2, Table 9), were still present on the sites, a few meters away from the plot margins. Their

(a)

(b)

(c)

Fig. 4 -- Sapindus oahuensis growing on different kinds of habitats: (a) on rocky talus substrate in plot 1, (b) on steep rockland in plot 4, and (c) on more stable rocky substrate outside plot 5.

TABLE 4. -- Evergreen seasonal forest, plot 7, dominated by native Diospyros and Metrosideros. Comparison of the 1950 and 1970 data, per 1000 m^2.

Species	1950		1970		
	Plants > 2.5 cm diam.		Plants > 2.5 cm diam.		Total
	Basal area (m^2)	No.	Basal area (m^2)	No.	no. of indiv.
A. Native species:					
*1. Diospyros sandwicensis	1.187	122	1.191	241	1343
*2. Canthium odoratum	0.104	35	0.176	99	941
*3. Metrosideros collina	0.695	14	1.197	42	44
*4. Pisonia umbellifera	0.291	10	0.420	13	58
*5. Psychotria hathewayi	0.293	36	0.080	11	48
6. Myrsine lessertiana	0.068	13	0.035	5	23
7. Dodonaea sandwicensis	0.005	3	0.039	17	24
8. Bobea elatior	0.042	5	0.041	8	14
9. Pouteria sandwicensis	0.075	2	0.059	3	24
10. Dracaena aurea	0.008	4	0.011	5	7
11. Pelea wawreana	0.004	1	0.013	4	5
12. Rauwolfia sandwicensis	0.004	1	0.010	2	2
13. Eugenia reinwardtiana	0.004	2	0.007	2	7
14. Santalum freycinetianum	0.058	2	0.052	2	2
15. Osmanthus sandwicensis	0.016	7	0.040	6	9
16. Tetraplasandra kaalae	0.068	3	0.032	1	1
17. Charpentiera obovata	0.004	2	0.001	1	1
18. Xylosma hawaiiensis	0.015	2	-----	---	----
19. Eugenia sandwicensis	-----	---	0.600	9	9
20. Pittosporum sulcatum	-----	---	0.002	1	17
21. Psychotria mariniana	-----	---	0.002	1	1
22. Diospyros hillebrandii	-----	---	0.005	1	1
23. Elaeocarpus bifidus	-----	---	0.009	4	4
B. Introduced species:					
24. Eugenia cumini	0.002	1	0.014	4	36
25. Psidium cattleianum	-----	---	0.009	6	100
26. Schinus terebinthifolius	-----	---	0.007	3	22
27. Aleurites moluccana	-----	---	0.025	4	4
28. Psidium guajava	-----	---	-----	---	2
29. Grevillea robusta	-----	---	-----	---	4

* The more common species

TABLE 5. -- Semi-deciduous seasonal forest, plot 6, dominated by native Diospyros and Canthium. Comparison of the 1950 and 1970 data, per 400 m^2.

Species	1950		1970		
	Plants > 2.5 cm diam.		Plants > 2.5 cm diam.		Total
	Basal area (m^2)	No.	Basal area (m^2)	No.	no. of indiv.
A. Native species:					
*1. Diospyros sandwicensis	0.111	22	0.653	231.3	818.7
*2. Canthium odoratum	0.115	78	0.069	27.3	125.3
3. Diospyros hillebrandii	0.043	11	0.015	2.0	2.0
4. Osmanthus sandwicensis	0.057	2	0.119	27.3	33.3
5. Colubrina oppositifolia	0.063	1	0.131	16.0	18.7
6. Reynoldsia sandwicensis	0.110	2	0.105	8.0	8.0
7. Eugenia reinwardtiana	0.032	2	0.002	2.0	37.3
8. Mezoneuron kavaiensis	0.019	6	0.007	1.3	8.7
9. Dracaena aurea	0.031	3	-----	-----	0.7
10. Erythrina sandwicensis	0.038	1	-----	-----	-----
11. Ochrosia sandwicensis	0.016	3	-----	-----	-----
12. Sapindus oahuensis	-----	--	0.055	2.0	23.3
13. Rauwolfia sandwicensis	-----	--	0.013	3.3	3.3
14. Myoporum sandwicense	-----	--	0.020	1.3	1.3
15. Pseudomorus brunoniana	-----	--	0.005	2.0	2.0
16. Antidesma pulvinatum	-----	--	0.007	1.3	1.3
17. Wikstroemia oahuensis	-----	--	0.001	0.7	4.7
18. Charpentiera obovata	-----	--	-----	-----	2.7
B. Introduced species:					
19. Eugenia cumini	0.084	14	0.135	4.0	27.3
20. Psidium cattleianum	-----	--	0.001	0.7	22.7
21. Psidium guajava	-----	--	0.001	0.7	8.7
22. Schinus terebinthifolius	-----	--	-----	-----	4.0
23. Leucaena leucocephala	-----	--	-----	-----	4.0
24. Grevillea robusta	-----	--	-----	-----	2.0

* The more common species

TABLE 6. -- Semi-deciduous seasonal forest, plot 5, dominated by native <u>Sapindus</u>. Comparison of the 1950 and 1970 data, per 1000 m^2.

Species	1950		1970		
	Plants > 2.5 cm diam.		Plants > 2.5 cm diam.		Total
	Basal area (m^2)	No.	Basal area (m^2)	No.	no. of indiv.
A. Native species:					
*1. Sapindus oahuensis	3.186	52	2.108	71.7	1632.5
2. Reynoldsia sandwicensis	0.643	5	0.230	2.5	3.3
B. Introduced species:					
3. Leucaena leucocephala	-----	--	0.118	30.8	479.2
4. Eugenia cumini	-----	--	-----	----	26.7
5. Schinus terebinthifolius	-----	--	-----	----	0.8
6. Aleurites moluccana	-----	--	-----	----	0.8

* The more common species

TABLE 7. -- Semi-deciduous seasonal forest, plot 4, dominated by native <u>Sapindus</u>. Comparison of the 1950 and 1970 data, per 400 m^2.

Species	1950 Plants > 2.5 cm diam. Basal area (m^2)	1950 Plants > 2.5 cm diam. No.	1970 Plants > 2.5 cm diam. Basal area (m^2)	1970 Plants > 2.5 cm diam. No.	1970 Total no. of indiv.
A. Native species:					
*1. Sapindus oahuensis	0.828	13	0.359	19.3	152.0
*2. Dracaena aurea	0.317	10	0.111	6.0	10.0
3. Osmanthus sandwicensis	0.253	4	0.051	3.3	3.3
4. Reynoldsia sandwicensis	0.001	1	0.002	1.3	1.3
5. Erythrina sandwicensis	0.068	1	0.064	0.7	0.7
6. Charpentiera obovata	0.007	2	-----	----	3.0
7. Neraudia angulata	0.004	2	-----	----	------
8. Nototrichium viride	0.002	1	-----	----	------
9. Bobea hookeri	-----	--	0.055	0.7	0.7
10. Diospyros sandwicensis	-----	--	0.015	1.3	182.7
11. Myoporum sandwicense	-----	--	0.005	0.7	0.7
12. Dodonaea eriocarpa	-----	--	0.001	0.7	1.3
13. Canthium odoratum	-----	--	0.005	3.3	32.7
14. Pseudomorus brunoniana	-----	--	0.003	1.3	1.3
B. Introduced species:					
*15. Leucaena leucocephala	0.068	34	0.338	272.0	6586.6
*16. Eugenia cumini	0.036	8	0.041	4.0	7.3
17. Schinus terebinthifolius	-----	--	0.016	4.0	24.0

* The more common species

TABLE 8. -- Seral _Erythrina_ stand, plot 3. Comparison of the 1950 and 1970 data, per 200 m^2.

Species	1950 Plants > 2.5 cm diam. Basal area (m^2)	1950 Plants > 2.5 cm diam. No.	1970 Plants > 2.5 cm diam. Basal area (m^2)	1970 Plants > 2.5 cm diam. No.	1970 Total no. of indiv.
A. Native species:					
*1. Erythrina sandwicensis	2.520	75	0.618	46.5	53.5
*2. Canthium odoratum	0.086	9	0.017	5.5	5.5
B. Introduced species:					
3. Schinus terebinthifolius	-----	--	0.010	2.5	41.0
4. Eugenia cumini	-----	--	0.032	1.0	1.5
5. Leucaena leucocephala	-----	--	-----	----	2.5

* The more common species

TABLE 9. -- Seral *Canthium*-*Leucaena* stand, plot 2. Comparison of the 1950 and 1970 data, per 1000 m^2.**

Species	1950	1970		
	Total no. of indiv.	Total no. of indiv.	Plants > 2.5 cm diam. No.	Basal area (m^2)
A. Native species:				
*1. Canthium odoratum	149	1125	190	0.441
2. Dodonaea eriocarpa	1	3	----	-----
3. Erythrina sandwicensis	1	----	----	-----
B. Introduced species:				
*4. Leucaena leucocephala	12	109,913	2038	1.161
5. Psidium guajava	2	58	----	-----
6. Schinus terebinthifolius	---	600	30	0.081
7. Psidium cattleianum	---	63	----	-----
8. Eugenia cumini	---	55	----	-----

* The more common species

** Because Hatheway recorded only the total number of individuals of each species, the comparison in this plot is based on total numbers instead of numbers of individuals larger than 2.5 cm in diameter only. This criterion is also used in determining the more common species in this plot.

TABLE 10. -- Seral Sapindus-Leucaena stand, plot 1. Comparison of the 1950 and 1970 data, per 30 m^2.

Species	1950		1970		
	Plants > 2.5 cm diam.		Plants > 2.5 cm diam.		Total
	Basal area (m^2)	No.	Basal area (m^2)	No.	no. of indiv.
A. Native species:					
*1. Sapindus oahuensis	0.008	8	0.151	4.2	224.4
2. Reynoldsia sandwicensis	0.002	1	-----	----	-----
B. Introduced species:					
*3. Leucaena leucocephala	0.045	31	0.030	10.2	39.0

* The more common species

exclusions are probably due to sampling error.

Individuals of two species (Neraudia angulata and Nototrichium viride) from plot 4 (Table 7) had disappeared. However, a young individual (below 2 m tall) of each of these two species was observed in the openings about 50 m away from the plot. The only species that had completely disappeared from the total slope area of each plot were Erythrina sandwicensis and Ochrosia sandwicensis from plot 6 (Table 5) and Reynoldsia sandwicensis from plot 1 (Table 10).

Additional native species were recorded only in the plots located inside the forest reserve (plot 7, Table 4, and plot 6, Table 5) and close to it (plot 4, Table 7). In plot 5 (Table 6), plot 3 (Table 8), plot 2 (Table 9), and plot 1 (Table 10), which are farther away from this forest reserve and therefore farther away from the seed sources of native species, no additional native species were recorded. A number of the additional native species were mature individuals and therefore were most likely already present in the plot area but not sampled by Hatheway. These are Eugenia sandwicensis from plot 7 (Table 4), Sapindus oahuensis, Rauwolfia sandwicensis, Myoporum sandwicense, Pseudomorus brunoniana, and Antidesma pulvinatum from plot 6 (Table 5), and Bobea hookeri from plot 4 (Table 7). All the other species, however, are young individuals (less than 10 cm in diameter), suggesting their recent arrival. These are Pittosporum sulcatum var. remyi, Psychotria mariniana, Diospyros hillebrandii, and Elaeocarpus bifidus from plot 7 (Table 4), Wikstroemia oahuensis and Charpentiera obovata from plot 6 (Table 5), and Diospyros sandwicensis, Myoporum sandwicense, Dodonaea eriocarpa, Canthium odoratum, and Pseudomorus brunoniana from plot 4 (Table 7). Among the mature individuals, the new records of individuals found in plots 7 and 4 are probably due to sampling error. The additional species in plot 6 were probably already present in this plot 20 years ago but not counted by Hatheway because they were still small individuals, less than 2.5 cm in diameter. At the present time these individuals are not particularly old, although they belong to the canopy trees. They are only slightly larger than 10 cm in diameter (except *Sapindus* which is about 30 cm in diameter).

Introduced species.

All the introduced species recorded by Hatheway are still found in their former plots. Furthermore, additions of new introduced species were recorded in almost every plot (except plot 1, Table 10), as shown in Tables 4 - 9. These additional species are small individuals, not larger than 10 cm in diameter. This suggests that all of them are newcomers, except for *Lantana camara* from plot 6 (Table 5). *Lantana* had been described by Hatheway as common undergrowth in the area of plot 6 but occurring as small individuals.

Regeneration and maintenance trends of species

Density changes.

An increase of basal area together with an increase in density means that the individuals of a species are growing and regenerating. An increase of basal area alone merely implies an increase in the diameter and stem area of pre-existing individuals. It does not imply regeneration, and therefore basal area cannot be used here. Increase in density, whether or not accompanied by an increase of basal area, usually reflects regeneration. However, the converse of this statement is not necessarily true. Natural death of the older and bigger trees in a species population may decrease the density and basal area values. But if seedlings and saplings of this species are present in abundance in this particular area, the observed decrease certainly does not indicate that the species is declining. A species can only be said to be declining if its old dead trees are not being replaced by its seedlings or saplings.

Changes in density can in theory provide information on regeneration. The results of the floristic changes suggest little error in matching the 1970 plots with their 1950 counterparts. However, in the comparison of the 1950 and 1970 data, the larger or smaller size of the 1970 plots may incorrectly increase or decrease the density value. This is especially true with the less common species that are usually found in clumps. Larger size of the plot does not necessarily yield larger number of individuals of these species.

For an accurate evaluation of which species listed by Hatheway are regenerating and maintaining themselves, the density comparison between the 1950 and 1970 data will only be made for the more common species. Based on the observation in the field, a more common species is here arbitrarily defined as a species that has one or more individuals per 100 m^2 larger than 2.5 cm in diameter in both the 1950 and 1970 analyses. These species are shown by asterisks preceding their names in Tables 4 - 10.

Among the more common species, increases in density are observed in *Diospyros sandwicensis*, *Canthium odoratum*, *Metrosideros collina* subsp. *polymorpha*, and *Pisonia umbellifera* from plot 7 (Table 4), *Diospyros sandwicensis* from plot 6 (Table 5), *Sapindus oahuensis* from plot 5 (Table 6), *Sapindus oahuensis* and *Leucaena leucocephala* from plot 4 (Table 7), and *Canthium odoratum* and *Leucaena leucocephala* from plot 2 (Table 9). These increases indicate that all these species are regenerating and maintaining themselves. Decreases in density, however, does not always mean that the species is declining. The regeneration trends of species in this group, i.e. *Psychotria hathewayi* (plot 7), *Canthium odoratum*, and *Eugenia cumini* (plot 6), *Dracaena aurea* and *Eugenia cumini* (plot 4), *Erythrina sandwicensis* and *Canthium odoratum* (plot 3), and *Sapindus oahuensis* and *Leucaena leucocephala* (plot 1), therefore are still unclear.

Population structures.

Figs. 5 - 11 show the population structures of the dominant species in plots 7 - 1. To evaluate the status of the introduced species, Figs. 5 - 11 also show the population structures of the important introduced tree species in these plots. A dominant species is here defined as a tree species that belongs to the group of more common species and forms part of the forest canopy. An introduced tree species is defined as important, when it has a density greater than 1.8 individuals per 100 m; the species must also occur in more than three size classes. It does not need to be part of the canopy as yet.

The interpretations of the developmental trends of these species are summarized in Table 11.

Table 11 shows that almost all the dominant native species and the dominant or important introduced species in each plot are perpetuating or regenerating themselves. The 1970 data of Metrosideros collina subsp. polymorpha (plot 7, Fig. 5) and Dracaena aurea (plot 4, Fig. 8) show few individuals in the height classes and irregular patterns, instead of decrease in log. frequency with increase in diameter classes. However, since this irregular pattern is similar to their distributional patterns in 1950, this evidence suggest that this irregular pattern of perpetuating themselves is characteristic to these two species. It suggests that for successful production of viable seeds, seed germination, and establishment of their seedlings they require certain triggers or they may have other methods of regeneration, other than by seedlings.

The comparison between the 1950 and 1970 diameter classes of Psychotria hathewayi (plot 7, Fig. 5) show large number of individuals lost in the last twenty years. Furthermore, its 1970 log. frequency in diameter classes shows a unimodal distribution, peaking at diameter class 4, suggesting that this species is not maintaining itself. Its 1970 log. frequency in height classes, however,

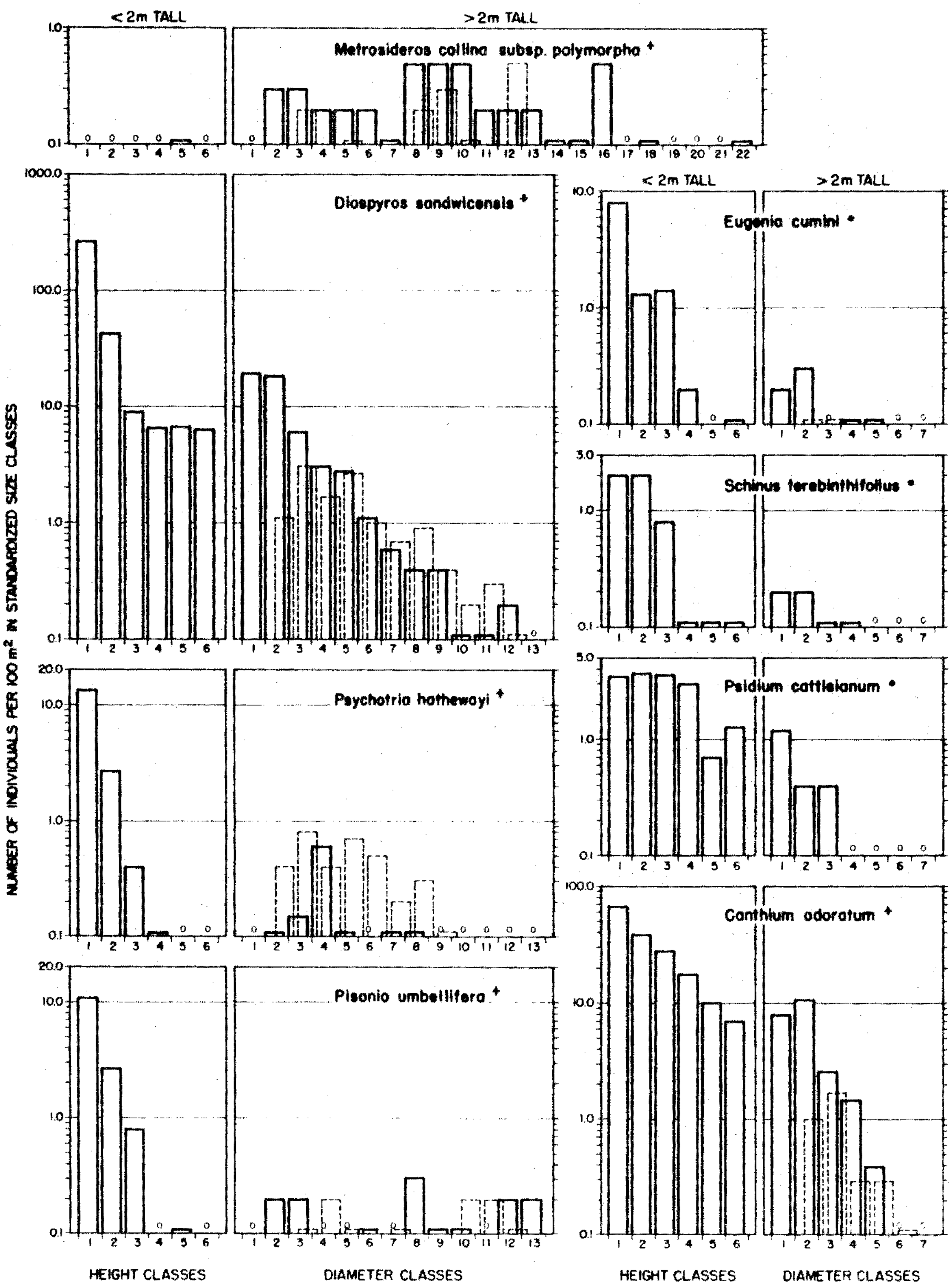


Fig. 5. Evergreen seasonal forest, plot 7. Population structure of native (+) and introduced (•) tree species. Histograms drawn with solid lines refer to the 1970 analysis, those drawn with dashed lines refer to the 1950 analysis. A zero (0) indicates that no individual is present in that size class in the 1970 analysis.

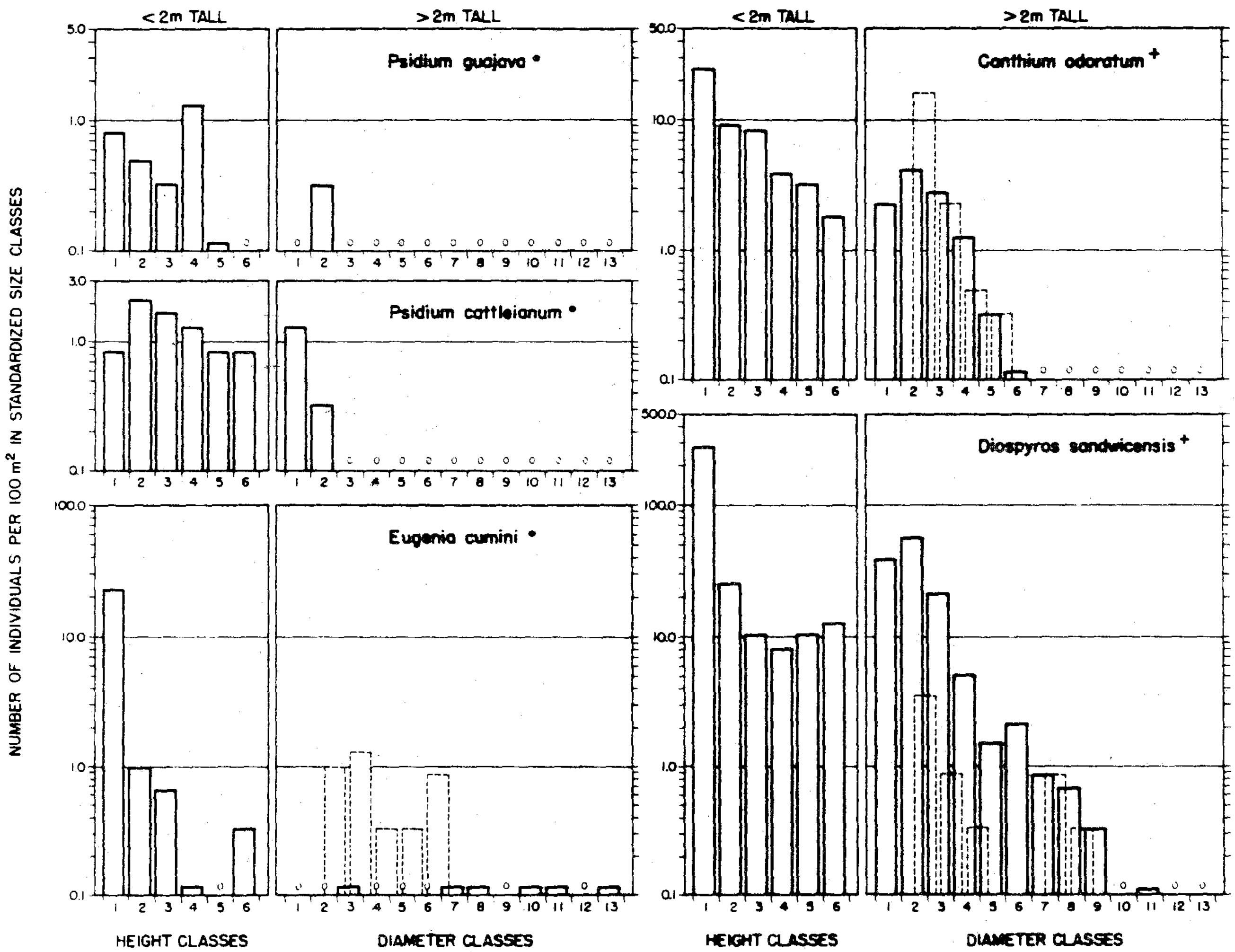


Fig. 6. Semi-deciduous seasonal forest, plot 6. Population structure of native (+) and introduced (•) tree species. Histograms drawn with solid lines refer to the 1970 analysis, those drawn with dashed lines refer to the 1950 analysis. A zero (0) indicates that no individual is present in that size class in the 1970 analysis.

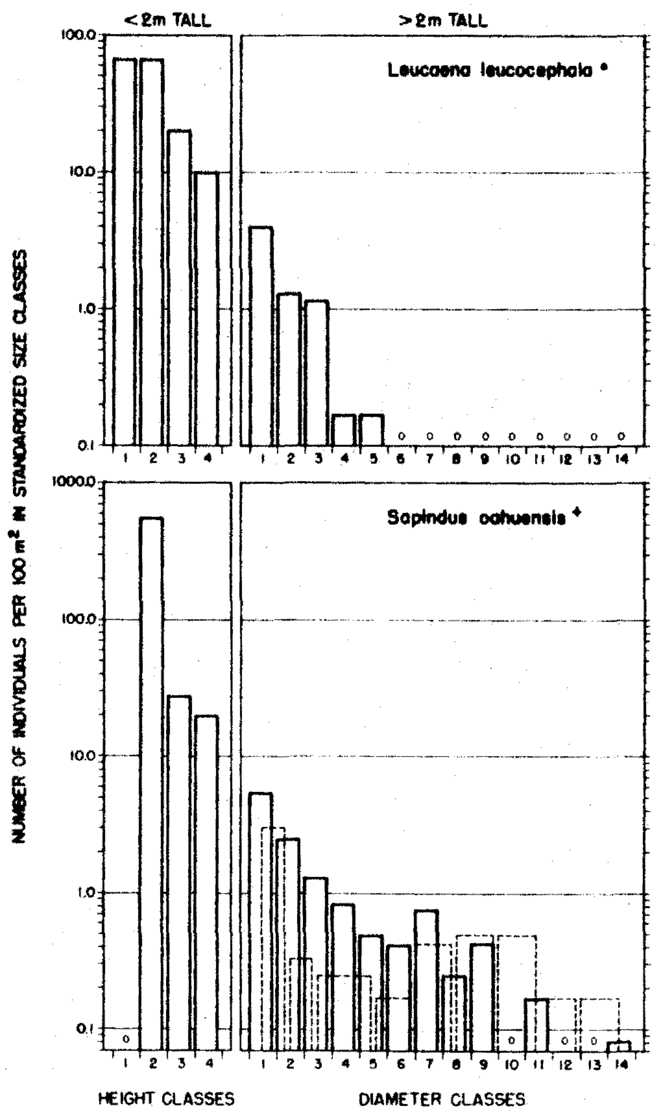


Fig. 7. Semi-deciduous seasonal forest, plot 5. Population structure of native (+) and introduced (•) tree species. Histograms drawn with solid lines refer to the 1970 analysis, those drawn with dashed lines refer to the 1950 analysis. A zero (0) indicates that no individual is present in that size class in the 1970 analysis.

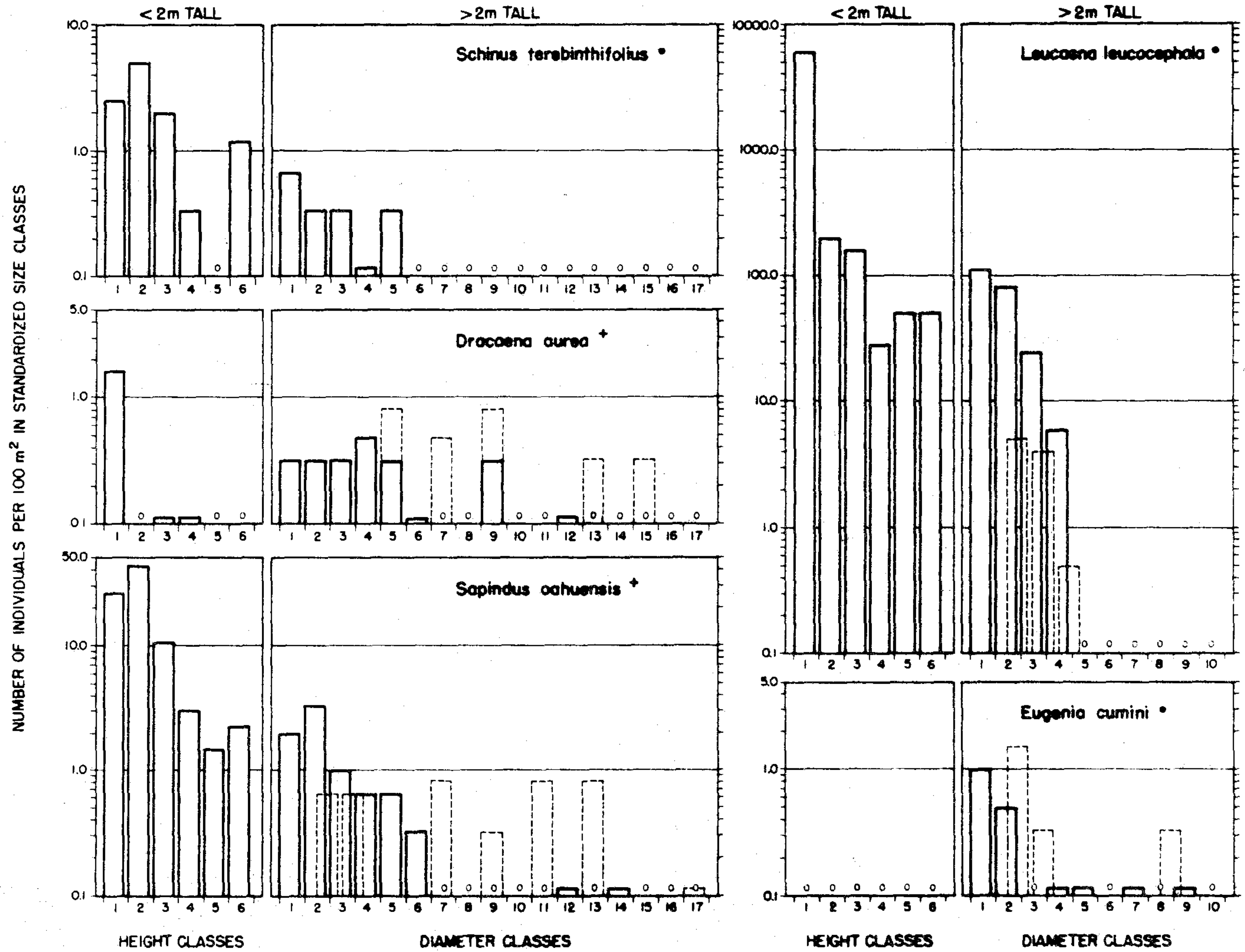


Fig. 8. Semi-deciduous seasonal forest, plot 4. Population structure of native (+) and introduced (•) tree species. Histograms drawn with solid lines refer to the 1970 analysis, those drawn with dashed lines refer to the 1950 analysis. A zero (0) indicates that no individual is present in that size class in the 1970 analysis.

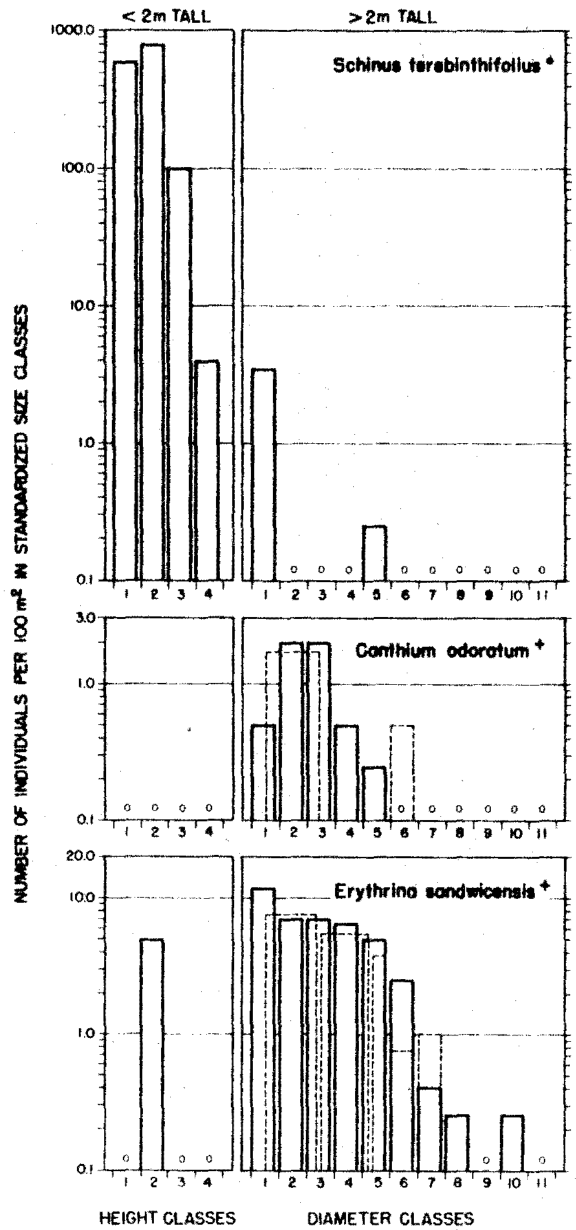


Fig. 9. Seral Erythrina stand, plot 3. Population structure of native (+) and introduced (•) tree species. Histograms drawn with solid lines refer to the 1970 analysis, those drawn with dashed lines refer to the 1950 analysis. A zero (0) indicates that no individual is present in that size class in the 1970 analysis.

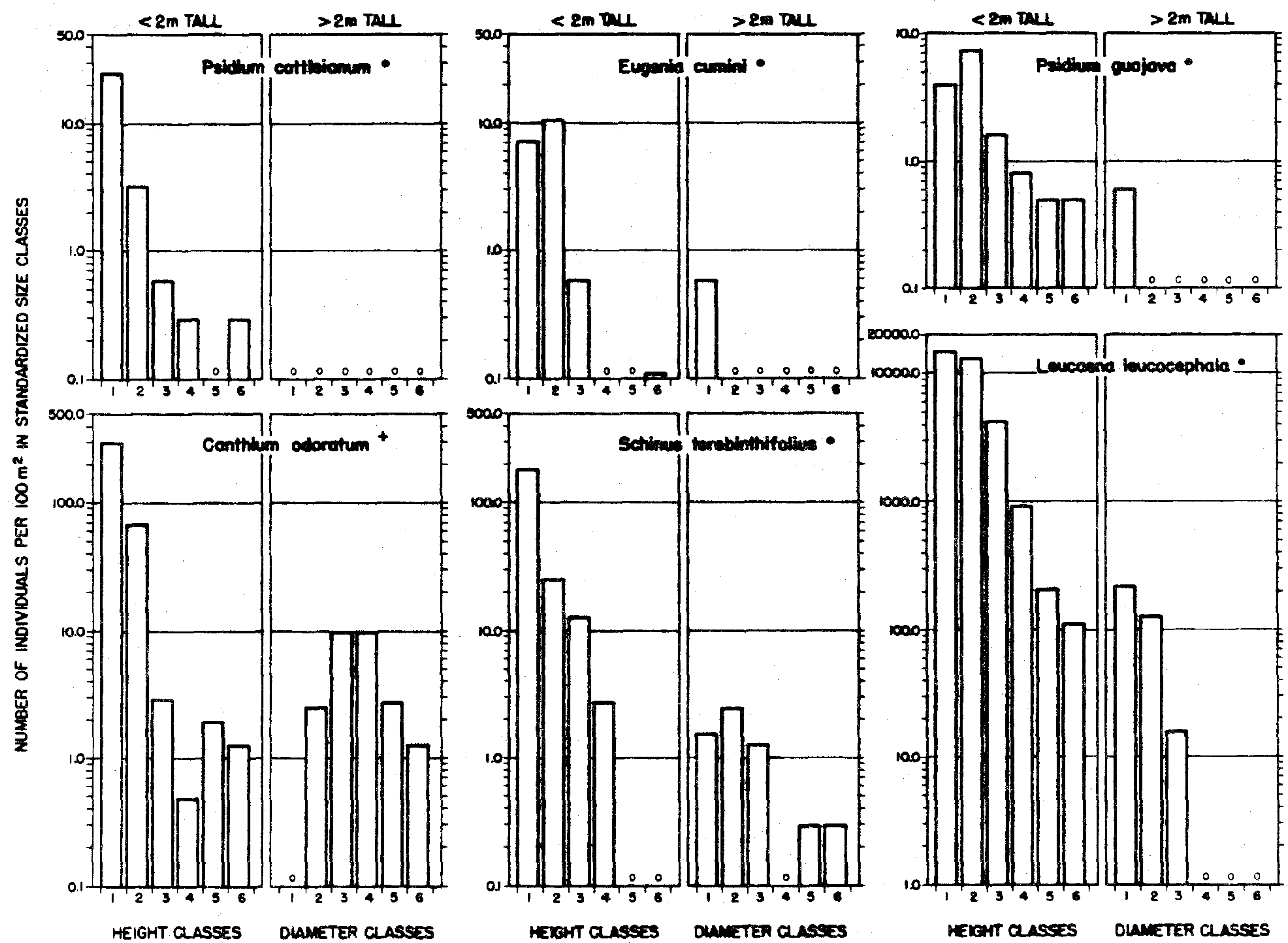


Fig. 10. Seral Canthium-Leucaena stand, plot 2. Population structure of native (+) and introduced (•) tree species. Histograms drawn with solid lines refer to the 1970 analysis, those drawn with dashed lines refer to the 1950 analysis. A zero (0) indicates that no individual is present in that size class in the 1970 analysis.

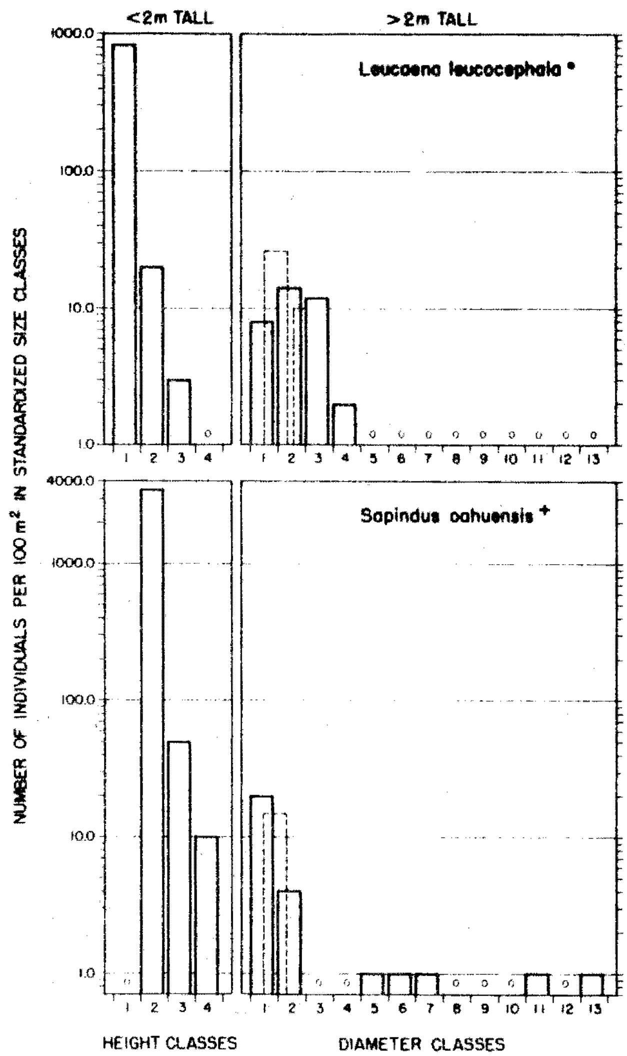


Fig. 11. Seral Sapindus stand, plot 1. Population structure of native (+) and introduced (•) tree species. Histograms drawn with solid lines refer to the 1970 analysis, those drawn with dashed lines refer to the 1950 analysis. A zero (0) indicates that no individual is present in that size class in the 1970 analysis.

TABLE 11. -- Population structure. Summary of the interpretations of the developmental trends of the dominant and important tree species in each of the seven plots.

Species	Perpetuating	Regenerating	Maintaining	Declining
Dominant native species:				
1. Metrosideros collina	(7)	------	------	------
2. Psychotria hathewayi	-------	(7)	------	------
3. Pisonia umbellifera	7	------	------	------
4. Diospyros sandwicensis	7, 6	------	------	------
5. Canthium odoratum	7, 6	------	------	3, (2)
6. Sapindus oahuensis	5, 4, 1	------	------	------
7. Dracaena aurea	(4)	------	------	------
8. Erythrina sandwicensis	-------	------	(3)	------
Dominant or important introduced species:				
9. Eugenia cumini	7	2	------	4, 6
10. Schinus terebinthifolius	7, 4, 3, 2	------	------	------
11. Psidium cattleianum	7, 6	2	------	------
12. Psidium guajava	2	6	------	------
13. Leucaena leucocephala	5, 4, 2	------	------	(1)

Note: The plot number in parentheses indicates that the interpretation of the developmental trend of the species in that plot is uncertain. They are discussed in the text for further clarification.

indicates that this species is regenerating itself. If this is an indication of better growing conditions, Psychotria may be able to perpetuate itself in this plot. If the absence of individuals between 100 - 200 cm tall (height class 5 and 6) means that its seedlings could not become established into bigger individuals, which may be the cause of the decreasing number of individuals in the diameter classes, the population structure of this species may suggest that this species is declining in this plot.

The population structure of Canthium odoratum (plot 2, Fig. 10), the only native tree species in this plot, shows a somewhat similar trend to Psychotria discussed above. Its diameter classes show a unimodal frequency distribution, peaking at diameter class 3 and 4, suggesting that, due to some factors occurring in the past, the number of Canthium individuals now found in diameter class 1 and 2 are much less than expected for a maintaining species. If this factor affected the population only for a short period, the decrease in log. frequency in the height classes may indicate that this species will still maintain itself. However, if this factor is still affecting the population and if the level or gradient of the distribution of height classes is partly caused by this factor, the population of the species might not be able in the future to produce as many individuals as are now found in the diameter class 3 or larger. Thus the species may be degenerating. Such a factor may, for example, be one that controls the production of viable seeds of this species. A large number of fruits and seeds of Canthium have been found to be badly infested and killed by the larvae of Orneodes objurgatella, a moth.

The 1950 and 1970 log. frequency in diameter classes of Erythrina sandwicensis in plot 3 (Fig. 9), the only native tree species in this plot, shows a similar decrease with increase in size classes indicating that this species is maintaining itself. However, the ground has been densely covered by the Melinis grass, which interrupts the seedling establishment of Erythrina. This is shown already by its low number of individuals below 2 m tall that are present in one height class only. The data show that Erythrina population in this plot may soon be reduced.

The population structure of Leucaena leucocephala in plot 1 (Fig. 11) shows a somewhat similar trend as that of Canthium odoratum in plot 2 (Fig. 10) or Psychotria hathewayi in plot 7 (Fig. 5).It shows a unimodal distribution in diameter classes, peaking at diameter class 2 and 3, and a decrease with increase in height classes up to height class 3 (less than 100 cm tall). Leucaena individuals taller than 2 m were found only at the margin of the plot, at the periphery of the Sapindus canopy. Although a large number of Leucaena seedlings were produced inside the plot, under the closed canopy of Sapindus, none of them become established individuals taller than 100 cm. These data suggest that when Sapindus is growing, perpetuating itself (Fig. 11), and taking over the area, Leucaena individuals cannot maintain themselves under the canopy of Sapindus. While native Canthium and Erythrina cannot maintain themselves in the other two seral plots discussed above, the native Sapindus is replacing the introduced Leucaena in this seral plot.

Vegetative regeneration.

In addition to plant regeneration from seed, field observations in this area suggest further that many of the native species show some types of vegetative regeneration which help them to maintain themselves in the area. However, vegetative regeneration was not observed among the introduced species. Among the native species, four types of vegetative regeneration were observed. These are:

(1) shoot forming type.-- In most cases, trees of Metrosideros collina subsp. polymorpha are found to have young shoots at the lower part of their stems.

These young shoots send roots to the ground, separate from the root system of the main stem. These shoots with their own roots are able to grow independently, even when the parent trees die. So far, this type of regeneration has been observed only in this species.

(2) broken stem type.-- _Dracaena aurea_ can vegetatively regenerate from broken off stems. _Dracaena_ stems are so brittle they easily break off when, for example, hit by rocks or falling branches. Most stems of individuals found in this closed forest and unstable ground were broken and some of the young individuals indicate that they originated by the sprouting of a broken stem. This was observed only in this species.

(3) basitonic branching type.-- Although _Osmanthus sandwicensis_ may grow as a single-stemmed tree, on unstable ground and steep slopes it usually occurs as a shrub-like tree. Each individual may consist of a number of stems of different sizes originating from a common base at ground level. Within each clump of this type of individual, it was rather common to find a dead stem or the remnant of a dead stem. Although seedlings of this species were observed occasionally, this species can maintain itself by continuous production of young stems from the base of old individuals. This regenerating mechanism was also observed in other native species, such as _Sapindus oahuensis_, _Diospyros sandwicensis_, _Bobea elatior_, _Myrsine lessertiana_, _Psychotria hathewayi_, and _Diospyros hillebrandii_.

(4) leaning stem type.-- _Pouteria sandwicensis_ is usually a single-stemmed tree. A mature tree of this species was observed leaning on the ground on a steep slope where anchorage was limited. Before the main stem of this tree died, a number of young shoots arose vertically from the basal part of the leaning stem. These shoots belonged to a number of different size classes. Downward these shoots produce roots separately. As in _Metrosideros_ and _Osmanthus_, these

young shoots will eventually continue their parent's life. This type of regeneration may also be observed in Diospyros hillebrandii and Sapindus oahuensis.

GENERAL DISCUSSION

The status of native dry forest

The floristic analysis shows that most of the species, both native and introduced, recorded by Hatheway are still present in their respective plots. New additions of native and introduced species to these plots were also recorded. However, although introduced species invaded almost all plots, native species invaded only plots 7 and 6 (which are located inside the Mokuleia Forest Reserve), and plot 4 (which is near the forest reserve, the main seed source of native species). No new native species invaded plots 1, 2, 3, and 5, which are rather far away from the forest reserve.

The results of the combined quantitative and qualitative approaches to the regenerating trends of species show that almost all dominant native species in each plot, except Erythrina sandwicensis in plot 3 and Canthium odoratum in plot 2, are regenerating and maintaining themselves. Since the future of the forest is determined by the dominant species they contain, it can be concluded that the native forest species in all plots, except 2 and 3, are perpetuating themselves.

The structural analysis indicates that changes of forest structure can be observed in plots 1, 2, 3, 5, and 6. The most significant changes of woody plants however, occurred only in plots 2 and 6. These changes are caused by the increasing numbers of plant individuals and species. In plot 6, these increases are mainly related to native species (Diospyros sandwicensis) whereas in plot 2 they are related to introduced species (Leucaena leucocephala and Schinus terebinthifolius). As has been indicated, plot 6 is located in the forest reserve where disturbance by cattle is absent and seed sources of native species are abundant. In contrast, plot 2 is located in the ranch area where disturbance by cattle is still present and the availability of seeds of native species is low. These facts not only suggest that seed sources of native species are important but also show that the elimination of the disturbance factor (grazing and trampling by cattle) is mandatory for a better development of native forest. Up to this point, all the above discussion supports Egler's and Hatheway's hypothesis that in the absence of disturbance and given the availability of seeds, native forests are able to suppress the incoming introduced species and then perpetuate themselves indefinitely. However, this ideal process is still subject to several other factors which may change the course of native forest development.

The ecological factors controlling the interactions of native and introduced species

Shade tolerance.

All introduced species recorded by Hatheway from his plots were still found in their respective plots. In addition, new invaders were observed in almost every plot. Except for *Grevillea robusta* (which is found in plots 6 and 7 as seedlings only) and *Eugenia cumini* (plots 4 and 6), the developmental trends of *Schinus terebinthifolius* (plots 2, 3, 4, 7), *Leucaena leucocephala* (plots 2, 4, 5), *Psidium cattleianum* (plots 2, 6, 7), *Psidium guajava* (plots 2, 6), and probably also *Eugenia cumini* (plots 2, 7), show that they are maintaining themselves in these areas. However, the regeneration of *Schinus* and *Leucaena* are confined to forest gaps or open areas only. This is different with *Psidium cattleianum* seedlings which are able to grow in the shade of their parent trees or in the shade of the native forest canopy (plots 6 and 7). Seedlings of *Psidium guajava* and *Eugenia cumini* seem to grow in-between these two extreme conditions. This suggests that, although the native species are maintaining themselves, they do not necessarily exclude all introduced species from growing with them. The shade-tolerant introduced species may remain in these forests, whereas the shade-intolerant introduced species will be restricted to open areas only.

The regeneration of Erythrina sandwicensis has been observed only in open areas, such as in the summer-deciduous Leucaena stand. In plot 3, the number of established Erythrina seedlings was reduced by the closed cover of Melinis minutiflora on the ground. In plots 2 and 4, Erythrina showed no regeneration. In plot 6, the only Erythrina tree recorded by Hatheway had disappeared from the area. These observations suggest that Erythrina is intolerant to shade and densification of plant cover tends to eliminate it from the area. Other shade-intolerant native trees probably also include Reynoldsia sandwicensis (which disappeared from plot 1 and did not regenerate in plot 6, although a few scattered seedlings were observed in the Leucaena stand close to plot 5) and some other native species, such as Myoporum sandwicense, Ochrosia sandwicensis, etc.

Soil water.

In plot 2, no plants were found growing under the closed canopy of mature Schinus terebinthifolius, not even Schinus seedlings. Within about 50 m, NE from this plot, a number of large, mature Schinus trees were associated with mature but dead individuals of Canthium odoratum. The Schinus individuals formed a closed canopy that covered an area of about 400 m^2. Outside this stand, where Schinus occurred as scattered individuals, Canthium individuals of the same size were growing vigorously. Seedlings of Schinus were quite abundant in the mixed stand of plot 2. Its regeneration trend and behavior in excluding other plants from growing underneath its canopy suggest that Schinus will take over the whole plot area. Since its own seedlings could not grow underneath its canopy, this pure single species stand tends to form plant cover without immediate replacement. Since *Canthium* can be observed in a much more shaded area (plot 6 and 7), the dead individuals noted above were most likely not killed from the lack of light. The cause may be competition for soil water or for something else. For management purposes, it is necessary to know what the true controlling factor is.

Biotic interference.

Twenty years ago, *Canthium* in plot 2 significantly outnumbered *Leucaena*. Now the situation is reversed. *Leucaena* produce large quantities of viable seeds. In contrast, many seeds of *Canthium* were infested by larvae of moth *Orneodes objurgatella*. In a number of cases, almost 100% of the fruits in each tree were destroyed by this moth. Zimmerman (1948) suspected that this moth is an introduced species. Although he and Swezey (1954) separately reported that the larvae of this moth heavily infested flower buds and fruits (seeds) of *Canthium* wherever this tree was found, so far, this type of damage was not seen on the trees found in less disturbed forests, such as in plots 6 and 7. This seed damage was found in the ranch area at lower elevations where cattle still act as the main source of disturbance. These observations suggest that physical disturbance of an area is not only followed by the invasion of introduced plant species but also by other biota that may be detrimental to the growth and development of native plant species.

An example of invasion by an introduced plant species that is detrimental to the reproduction of native forests is shown by *Melinis minutiflora* in plot 3. As the cover of this grass increased, it reduced the seedling establishment of *Erythrina*. Because of this, it was suggested earlier that the *Erythrina* population in this stand will ultimately be wiped out.

Melinis minutiflora is mostly found in open grassland or in ecotones of grass and scrub or grass and forest vegetations (Kartawinata 1971). It has never been found underneath a closed canopy. The dead Melinis observed in this plot during the spring suggests that this grass is intolerant to shade.

As shown in Table 6, plot 3 is invaded by Schinus terebinthifolius, which occurs in-between the patches of Melinis cover. At the present time, most of the Schinus individuals are still young and therefore there is very little cover. Its regeneration trend (Fig. 6) shows that Schinus is maintaining itself in this area. Therefore, when these individuals become mature, there is a good chance that they will form the major component of the woody plant cover as found next to plot 2. As Melinis is intolerant to shade, this grass will most likely be eliminated from the stand. If undisturbed, the future of this stand will most likely be a closed canopy stand dominated by the introduced Schinus terebinthifolius. In a sense, these observations support Degener's (1930) and Carlquist's (1965) view that the introduced biota are very aggressive.

Habitat variations.

Hatheway's analysis in plots 1, 2, and 3 showed that native species were able to invade plant communities composed of introduced species. The present analysis however, has failed to show that all the three native species in these three plots are maintaining themselves. It is only in plot 1 that the native species (Sapindus) is perpetuating itself. Here, Sapindus is also slowly spreading and replacing the surrounding introduced Leucaena stand. In plots 2 and 3, the native Canthium and Erythrina will most likely be replaced by the introduced Schinus. Due to the aggressiveness of this species, Hatheway's prediction that a mixed forest will be the end result of succession in plot 2 will probably not be true in the near future. These different results of development of stands composed of native species are perhaps not only due to the new influx of woody species but they may be also due to the variation in habitats. Hatheway's plots 2 and 3 are located on deep Humic Latosol soil whereas his plot 1 is on rough rocky talus material.

The above examples, which were based on limited observations, show only some of the eco-physiological properties of the available species. Other properties, such as the number of seeds produced, their viability, and dispersal mechanisms have not been given enough consideration by earlier studies -- not even in the present study. For a thorough study of the forest development, all these factors therefore should be properly evaluated.

The possible reclamation of the *Leucaena* stand in the lowland of Oahu with native tree species

As pointed out by Egler (1942, 1947) and Hatheway (1952), *Leucaena* stands are susceptible to invasion by other woody plant species. The present analysis in plot 2 shows that *Schinus* is one of these species, which moreover should be given special attention because of its potential to form plant cover without immediate replacement. Since *Leucaena* stands cover extensive lowland areas of Oahu, they should be protected from the invasion of *Schinus* to avoid the possible danger of soil erosion in the future.

At present time, most *Leucaena* stands can be classified as idle lands. The small size of the Hawaiian Islands, the increasing size of their populations, and the greater demand for natural recreation areas, suggest that these idle lands should be utilized. In general, one can walk more easily in the unmanaged forest composed of native species rather than in forest composed of introduced species, such as in the *Psidium cattleianum* and the *Leucaena* stands. In addition, native forests are capable of perpetuating themselves. The ability of native tree species to regenerate vegetatively on the unstable ground indicates that they are better adapted to the rugged Hawaiian topography than the introduced species. The replacement of Leucaena with native tree species might also invite the return of the associated native Hawaiian flora and fauna to the lowland areas. For these reasons, further research on this matter should be undertaken.

In the present analysis, the data from plots 1 and 5 show that the native Sapindus oahuensis is able to invade and replace the surrounding Leucaena and then maintain itself in that area. Sapindus saplings that invaded the Leucaena stand (plot 1) twenty years ago are growing and maintaining themselves. They form a small stand of closed native forest in the matrix of the Leucaena stand. This Sapindus stand excludes Leucaena from growing underneath its canopy. This was also observed in the Sapindus stand in plot 5.

Data from other plots show that native species are able to perpetuate themselves under the canopy of other native species, including Sapindus. It has also been shown that Sapindus can grow in different types of habitats and can adapt itself to the most extreme physical conditions as found for example, in the rocky talus substrate in plots 1 and 5. Therefore, as a means for reclaiming the lowland areas with native forest trees, Sapindus oahuensis seems to be one of the promising species. However, seeds of this species do not spread far from their parent trees and, so far, no distributing agent is known except man. Experimentation on how such a reclamation project could be carried out effectively needs further study.

CONCLUSIONS

To understand the development of dry forests in the Mokuleia area, the interaction between the native and introduced species that they contain could not be reduced to one simple formula (Degener-Carlquist or Egler-Hatheway).

Under undisturbed conditions, native forests are able to perpetuate themselves and suppress the invasion of introduced species. However, introduced species may take over in dominance where their eco-physiological properties fit with those of a niche not occupied by native species. Since seeds of shade-intolerant introduced species, such as Leucaena leucocephala, are more readily available than seeds of shade-intolerant native species, such cases of invasion are mostly found in man-disturbed areas that are opened up. In time, without further disturbance, native and alien shade-tolerant species have an equal chance to replace these pioneer stands. The results, however, depend on the availability of viable seeds (availability of parent trees, seed dispersal mechanisms, seed destruction -- such as by moth larvae on Canthium seed), the habitat, and the eco-physiological properties of the available species (the ability to compete for light, water, food, etc. among themselves). Taking these factors into consideration, the problem of native vs. alien species presents itself in a quite different context from Degener-Carlquist's and Egler-Hatheway's formulas.

The extent to which introduced tree species have taken over the Mokuleia forest area, or the extent to which native tree species have come back and replaced the introduced forest stands, was not answered by Hatheway's analysis and is not answered in the present re-analysis of his plots. Only properly designed systematic samplings of the forest area will give a reliable answer to this question.

ACKNOWLEDGEMENTS

I am especially indebted to my able and hard-working field assistant Glen Spence. D. T. Rickard (English Language Institute) provided valuable help in the initial writing of this paper. G. McNicoll (Population Institute, East-West Center), D. J. C. Friend, C. H. Lamoureux, and C. W. Smith (all from the Botany Department, University of Hawaii) offered generous advice and critical reading of the manuscript. My major professor, D. Mueller-Dombois, gave his continuing guidance, encouragement and support.

Acknowledgement is also made to Steve Montgomery for isolating and identifying the moth, to T. Nakata for drafting the figures, and to W. J. Hoe for many valuable discussions.

The aerial photographs of the area were supplied by the Towill Corporation. Access to papers related to the history of the Mokuleia Forest Reserve was provided by Hawaii State Forestry Division. Excellent cooperation and access to the study area were given by E. Silva and G. J. Cran, managers of Kaala and Mokuleia Ranches respectively.

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